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THE COARSE WRINKLE LAYER OF PALAEOZOIC AMMONOIDS: NEW EVIDENCE FROM THE EARLY CARBONIFEROUS OF MOROCCO

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Abstract: The wrinkle layer is a dorsal shell structure occurring in a number of ammonoids, but its function is still debated. Here, we describe, from Moroccan material of the Early Carboniferous species *Maxigoniatites saourensis* (Pareyn, 1961), the most conspicuous wrinkle layer known within the Ammonoidea. This additional shell layer occurs in the ventrolateral portion of the adult body chamber and forms continuous lamellae, which range about two millimetres into the lumen of the body chamber. Possible functions are discussed and the most likely interpretation for the structure is 'fabricational noise', which is related to the coarsening of the shell ornament of the terminal body chamber.

Key words: Ammonoidea, Early Carboniferous, coarse wrinkle layer, Morocco, fabricational noise.

THE wrinkle layer or Runzelschicht (Keyserling 1846) is a shell structure in ammonoids that occurs dorsally within the body chamber and is attached to the preceding whorl of the ammonoid. This structure has not been studied extensively; the most comprehensive investigations of this structure were carried out in the second half of the twentieth century by Walliser (1970), House (1971), Senior (1971), Tozer (1972), Bayer (1974), Doguzhaeva (1981), Korn (1985), Doguzhaeva and Mutvei (1986) and Kulicki *et al.* (2001). Most of these investigations focused on the morphology and distribution of the varied patterns of interest, which occur in several ammonoid taxa at different times in the geological past. Similar structures were described in Devonian bactritoids by Kröger *et al.* (2005) and in Carboniferous bactritoids by Mapes (1979).

During the past decade, extensive ammonoid collections from a number of Early Carboniferous stratigraphic horizons at locations within Morocco have yielded a variety of spirally ornamented ammonoids (Korn *et al.* 1999, 2005, 2007; Klug *et al.* 2006), some of which possess extraordinarily coarse shell structures on the dorsal area within the terminal body chamber. We conclude that these deposits must be an extreme form of the wrinkle layer, which usually is composed of faint lirae in other ammonoids. The description and discussion of the formation and possible function of this coarse wrinkle layer is the subject of this report.

MATERIAL

A total of 80 specimens of the species *Maxigoniatites saourensis* (Pareyn, 1961) from a single horizon in the late Viséan Mougui Ayoun Formation south of Dar Kaoua and Mougui Ayoun (Tafilalt, Eastern Anti-Atlas) are available for study (Fig. 1), most of which show at least some traces of the wrinkle layer. Almost all specimens are preserved three dimensionally in sideritic nodules with the shell wall being silicified. Most of the specimens were weathered out of the nodules by aeolian erosion and exhibit very good external shell preservation. Of particular interest are those specimens, in which parts of the body chamber were still preserved and filled with sideritic sediment. This sediment can be removed by the use of acid dissolution and careful application of air-abrasive techniques in the laboratory. This method of preparation allowed the excavation of the three-dimensional wrinkle layer with its unique wrinkle layer structure.

DESCRIPTION OF THE COARSE WRINKLE LAYER

The following description of the wrinkle layer patterns is mainly based on the three well-preserved specimens MB.C.22601, MB.C.22602 and MB.C.22603 (Figs 2–4),

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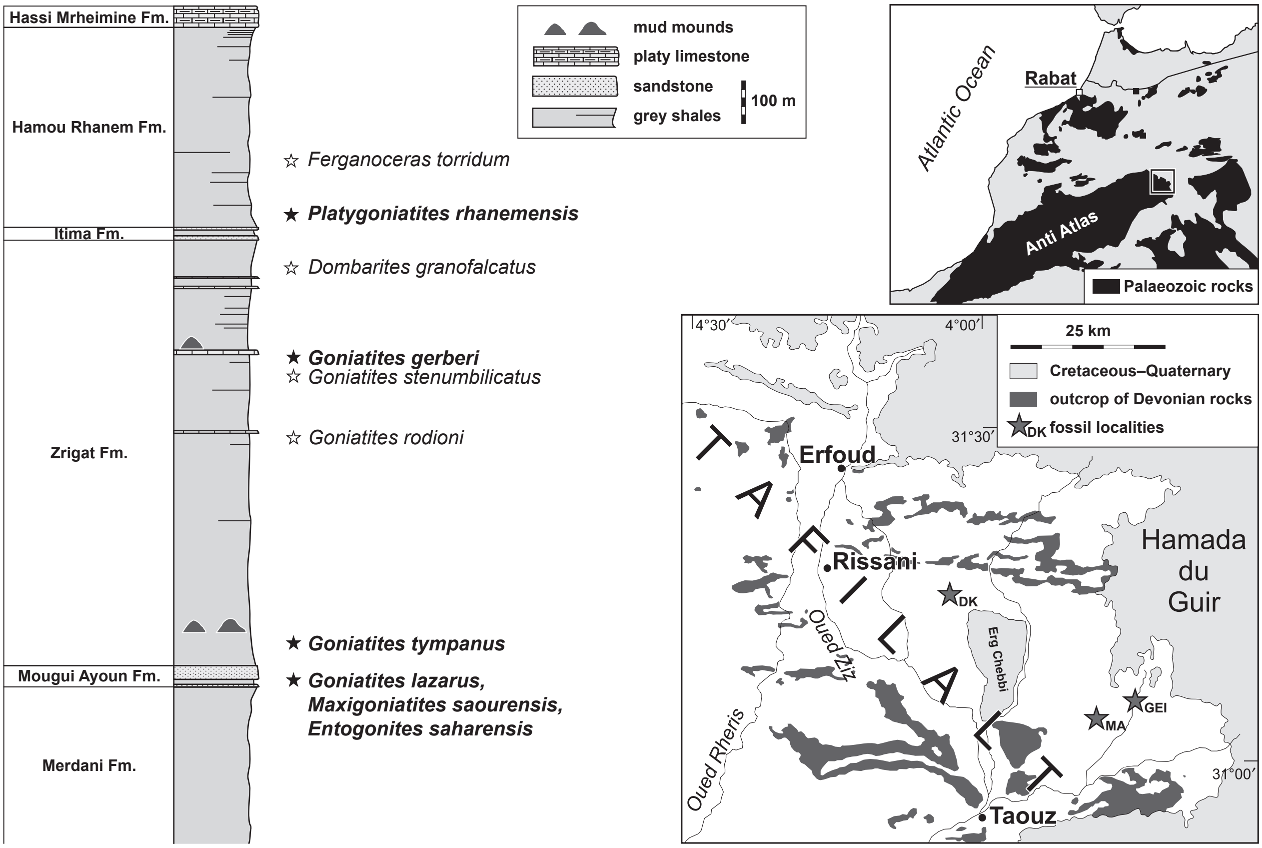

FIG. 1. Geographical map with the position of the localities with ammonoids showing the coarse wrinkle layer and stratigraphic column of the Viséan rock succession in the Eastern Anti-Atlas of Morocco (horizons under study in bold). DK, Dar Kaoua oasis; MA, Mougui Ayoun; GEI, Gara el Itima.

stored in the cephalopod collection of the Museum für Naturkunde, Berlin. Additional specimens showing these patterns are available in the repository collections at Ohio University.

Specimen MB.C.22601 is a well-preserved but somewhat fragmented individual, which had a diameter of *c.* 105 mm. It is thus among the largest known specimens of the species and may therefore be regarded as adult. The specimen consists of a partial body chamber of which about 120 degrees is preserved on the side of the specimen figured here (Fig. 2A), and which is more completely preserved on the side, which is not figured. Removal of parts of the body chamber by abrasion has exposed portions of the shell-covered phragmocone.

The shell ornament is excellently preserved on both the body chamber and the phragmocone; it consists of delicate and almost equidistant sinuous growth lines, of which six to eight occur within an area of one millimetre on the middle of the flanks. Periodically, the growth lines are slightly strengthened, and this probably indicates growth interruptions (e.g. Bucher 1997). The course of the growth lines is biconvex with a shallow projection on the umbilical wall, a low sinus on the umbilical margin, a low and wide dorsolateral projection, a wide and shallow lateral sinus, a moderately high and wide ventrolateral projection and a moderately deep ventral sinus. The spiral ornament is much coarser than the radial growth lines, with spiral lines varying significantly between 0.4 and 1.6 mm distance from each other. The thickness of the spiral lines is also very variable; they are granulated at the crossings with the growth lines.

The wrinkle layer is visible on the dorsal whorl zone where the body chamber is eroded and the filled sedimentary matrix has been removed (Fig. 2). The extremely prominent wrinkle layer pattern covers the lateral and ventrolateral portion of the dorsal whorl zone; the structure wedges out towards the umbilicus and towards the ventrolateral shoulder. In the inner flank area, the wrinkle layer begins with small isolated patches at about 6 mm distance from the umbilical seam. Another two millimetres further towards the midflank, the wrinkles form continuous lamellae, which are apically directed and in some places form a honeycomb-like pattern. The most conspicuous wrinkle layer occurs on the outer flank; here, the crests of the wrinkle layer are up to 2 mm high and have a flake-like shape with the crest directed towards the

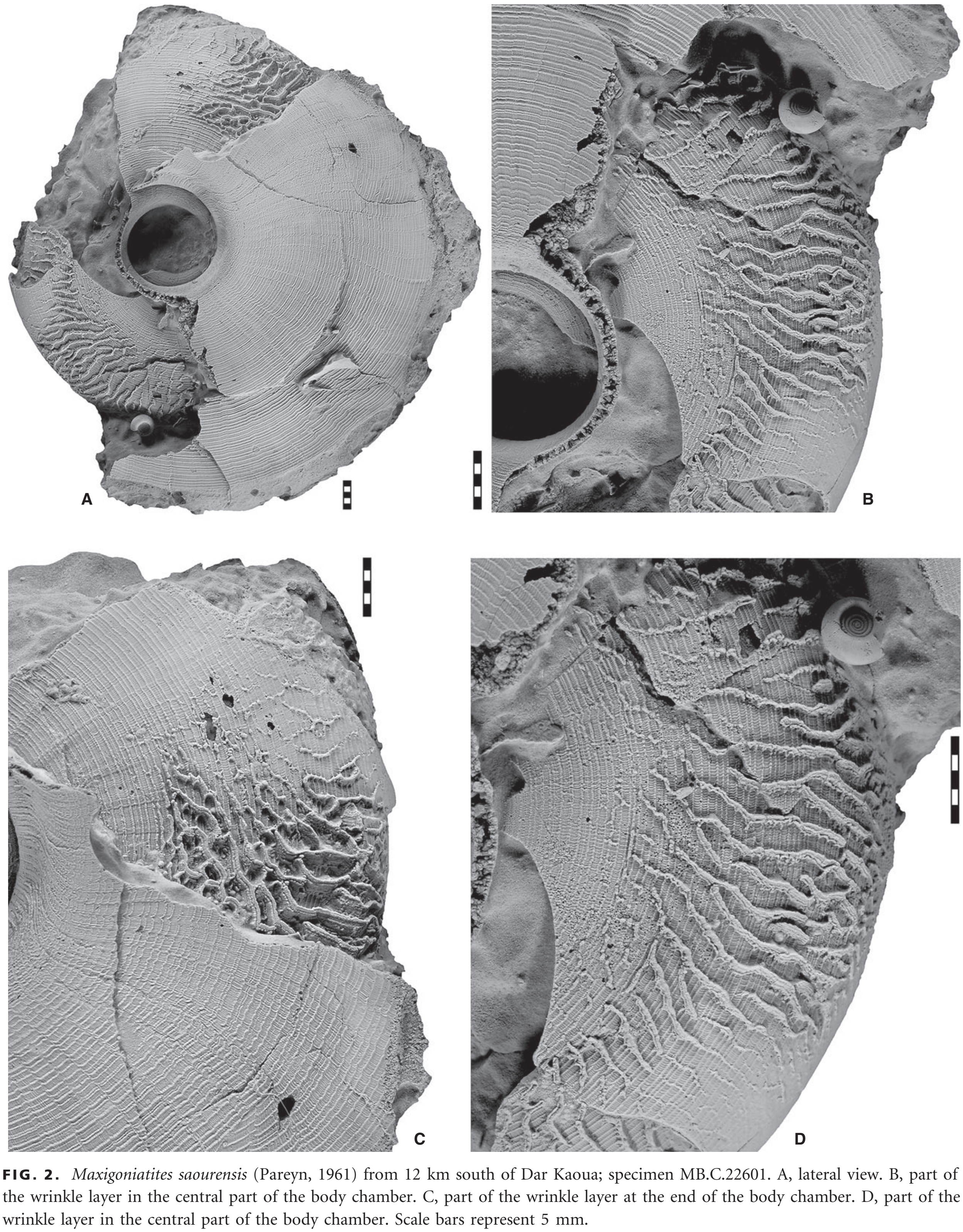

FIG. 2. *Maxigoniatites saourensis* (Pareyn, 1961) from 12 km south of Dar Kaoua; specimen MB.C.22601. A, lateral view. B, part of the wrinkle layer in the central part of the body chamber. C, part of the wrinkle layer at the end of the body chamber. D, part of the wrinkle layer in the central part of the body chamber. Scale bars represent 5 mm.

aperture. These wrinkles appear somewhat granulated and possess growth lines, which vary in their strength. The alternation of fine and coarse growth lines on the wrinkles can be duplicated on a number of the wrinkles (Fig. 2B, D). The view on the crests of the wrinkles shows that they consist of two or more lamellae fused together.

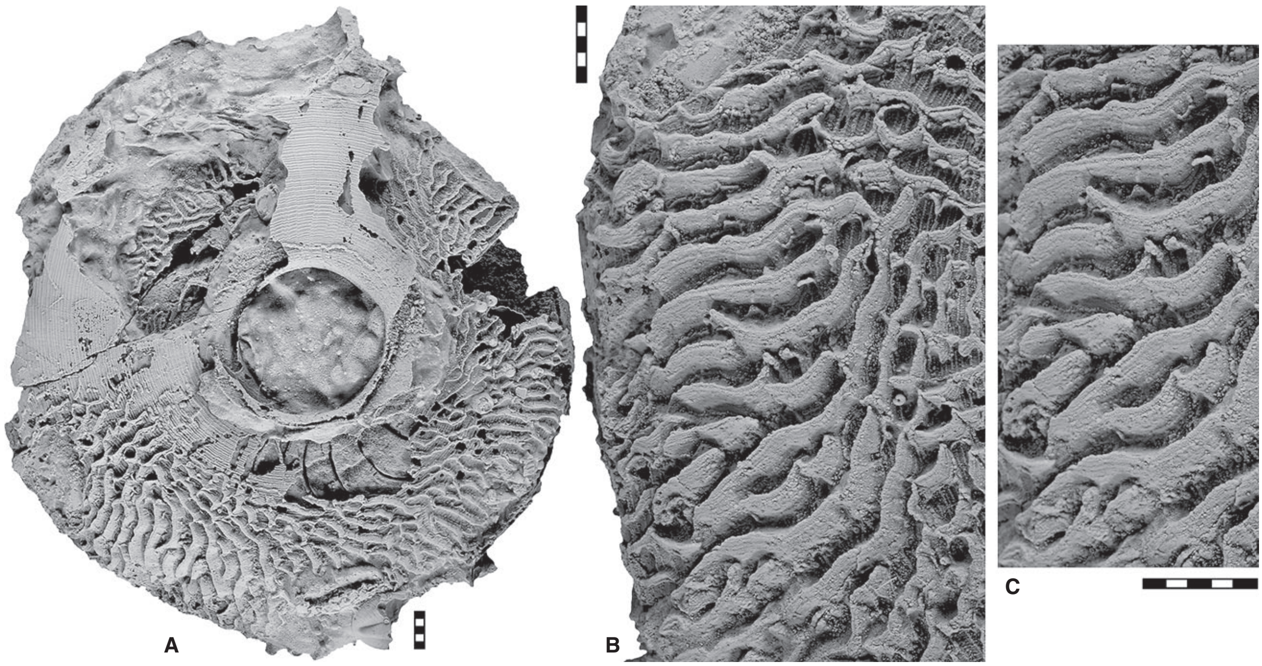

FIG. 3. *Maxigoniatites saourensis* (Pareyn, 1961) from 12 km south of Dar Kaoua; specimen MB.C.22602. A, lateral view. B, part of the coarse wrinkle layer in the central part of the body chamber. C, part of the wrinkle layer in the central part or the body chamber. Scale bars represent 5 mm.

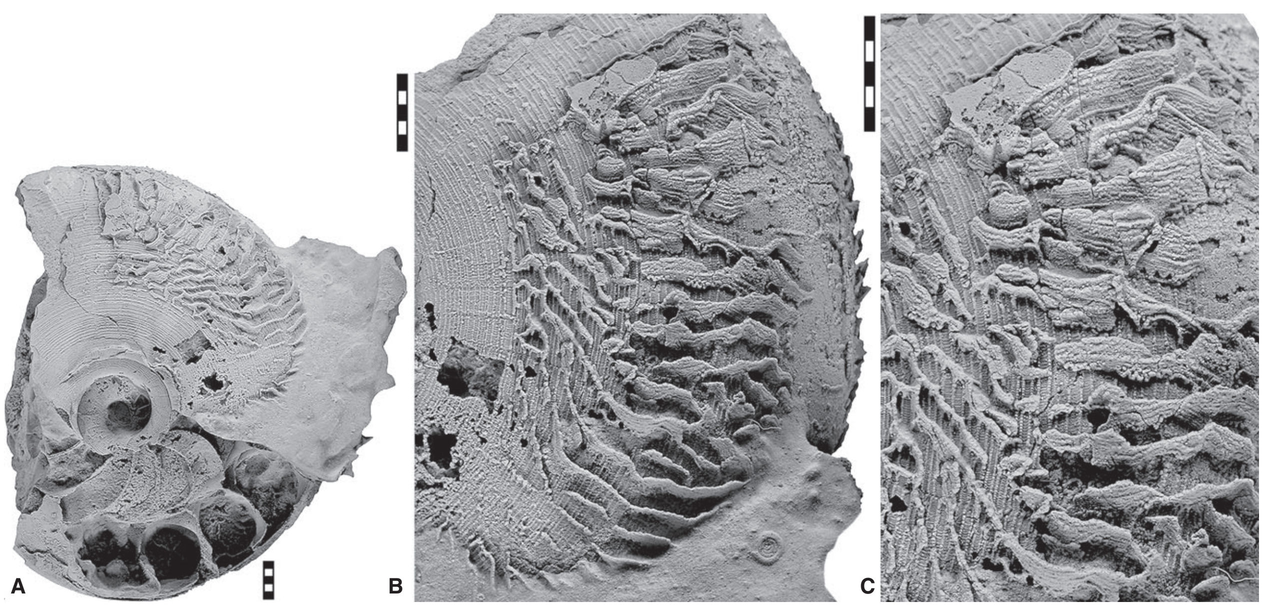

FIG. 4. *Maxigoniatites saourensis* (Pareyn, 1961) from 12 km south of Dar Kaoua; specimen MB.C.22603. A, lateral view. B, part of the coarse wrinkle layer in the central part of the body chamber. C, part of the coarse wrinkle layer in the central part or the body chamber. Scale bars represent 5 mm.

It is apparent that formation of the wrinkle layer preferentially started on the granulation of the spiral lines of the shell ornament (Fig. 2C). At the apertural end of the wrinkle layer, the initiation of new wrinkles begins by using the spiral lines as depositional starting points.

Specimen MB.C.22602 is also a fully adult specimen with an original conch diameter of about 100 mm (Fig. 3A). It is much less complete than specimen MB.C.22601, with most of the body chamber being absent and showing some lateral crushing. The wrinkle layer can be seen on a complete volution of the dorsal whorl zone, and it is much more strongly developed than in specimen MB.C.22601.

The wrinkles begin about 8 mm from the umbilical seam on the inner flank and form blister-like structures or occasionally small compartments, with the elements being radial or apically directed. On the midflank, they turn into elongate, more radial elements, which bifurcate or fuse. Here, they appear like sand ripples, with distances of about 2 mm between the elements. The wrinkles are elevated about three millimetres into the lumen of the body chamber. They possess growth lines of varying strength (Fig. 3B, C).

Specimen MB.C.22603 is smaller with a phragmocone diameter of 60 mm (Fig. 4). It shows a very similar wrinkle layer pattern to the other two specimens with an area near the umbilical seam with very small patches situated on the spiral lines, with mainly apically directed wrinkles on the inner flank and with the coarsest structures on the outer flank (Fig. 4).

THE DISTRIBUTION OF THE COARSE WRINKLE LAYER

Phylogenetic distribution

Two independent clades of Palaeozoic ammonoids display the coarse wrinkle layer, the family Maxigoniatitidae (with the genera *Maxigoniatites* and *Beyrichoceras*) and the family Goniatitidae (with the genera *Goniatites* and *Neogoniatites*) with its phylogenetic descendant the Delepinoceratidae (genus *Platygoniatites*). It is remarkable that, within the two clades, the coarse wrinkle layer has a rather patchy distribution and that some subclades do not develop this structure.

According to our data, the coarse wrinkle layer is a structure that cannot be interpreted as an apomorphic character. It occurs independently in various ammonoid lineages and is highly homoplastic despite the fact that it is very similar in its morphological expression. However, in most major ammonoid clades, coarse wrinkle layers have never been documented.

Ontogenetic distribution

In the material of *M. saourensis* from Dar Kaoua, the coarse wrinkle layer is seen only in large specimens that were fully mature, and where the diameter of the phragmocone was at least 60 mm (corresponding to a total diameter of the conch of about 90 mm). Similarly, the specimens of *Goniatites* with the coarse wrinkle layer from the various occurrences belong to the largest of their populations. It can be concluded that the structure is probably a mature modification and indicates the end of somatic growth of the animals. This is also supported by the occurrence of the wrinkle layer in Middle Devonian *Maenioceras*, where especially large specimens show this feature well (although less strongly than in their Carboniferous counterparts).

Morphological distribution

All the species with the coarse wrinkle layer share a few characters, in spite of their phylogenetic distribution. One of these characters is the presence of more or less fine spiral ornament (Fig. 5). This does not mean, however, that all spirally ornamented late Viséan ammonoids show the coarse wrinkle layer. It is, for instance, not known from the families Neoglyphioceratidae and Cravenoceratidae or from the subfamily Arnsbergitinae (which is within the Goniatitidae). The list of genera and species that possess the coarse wrinkle layer demonstrates that this structure occurs preferentially in species with delicate spiral ornament, but not in those taxa characterized by coarse spiral lines. This is probably the reason why it is obviously absent in genera such as *Lusitanoceras* and *Dombarites*.

Another, but probably much less strict, precondition for the coarse wrinkle layer is a low aperture that implies a long body chamber. In *M. saourensis*, the body chamber has a length of more than one volution, with a whorl expansion rate of less than 1.60 in the terminal growth stage. Similarly, all species of *Goniatites*, *Neogoniatites* and *Platygoniatites* are longidome. It is worth mentioning, however, that there are also longidome late Viséan ammonoids that do not possess the coarse wrinkle layer.

A character that is closely linked with the low aperture is the very narrow space between the ventrolateral wall of the preceding whorl and the dorsolateral wall of the last whorl. Finally, none of the species with the strong wrinkle layer have a wide umbilicus.

Stratigraphical distribution

Most of the ammonoid species with the coarse wrinkle layer come from a limited stratigraphic range within the late Viséan (Fig. 6). *Maxigoniatites*, *Beyrichoceras* and *Goniatites* are restricted to the Asbian and earliest Brigantian of the British chronostratigraphic scheme and middle late Viséan in the standard scheme. *Platygoniatites* and *Neogoniatites* are stratigraphically younger and occur in the latest Viséan close to the Viséan–Serpukhovian boundary.

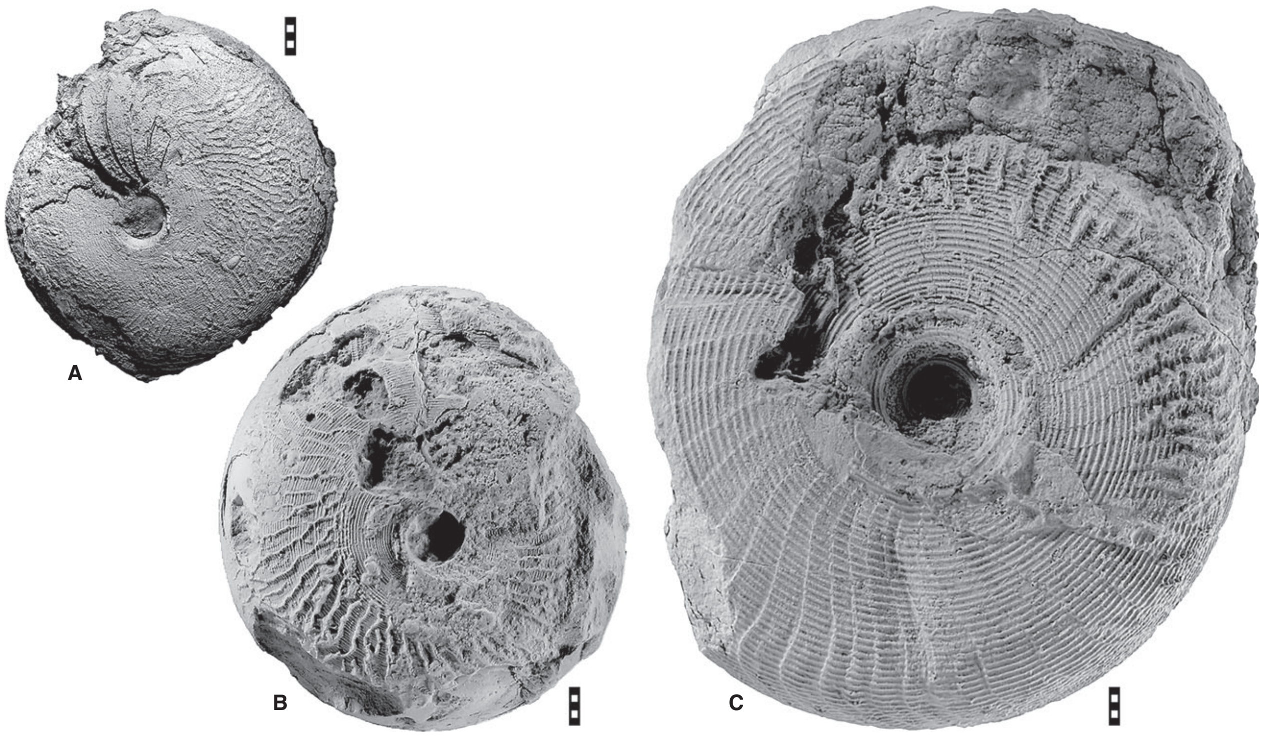

FIG. 5. Ammonoids with the coarse wrinkle layer. A, *Goniatites spirifer* Roemer, 1850 from the Glenne Valley, near Scharfenberg (Rhenish Mountains, Germany); latex mould MB.C.22604. B, *Goniatites tympanus* Korn *et al*., 2007 from the area of Erfoud (Anti-Atlas, Morocco); specimen AMNH 46716 (Landman Coll.). C, *Platygoniatites rhanemensis* Korn & Ebbighausen, 2006 from Gara el Itima (Anti-Atlas, Morocco); specimen MB.C.9079.16. Scale bars represent 5 mm.

Geographical distribution

Wrinkle layer structures similar to those described here in specimens of *M. saourensis*, but usually much less prominent, have been recorded from a number of other ammonoid occurrences. Such structures are known from most of the geographical regions in which representatives or close relatives of the families Maxigoniatitidae and Goniatitidae are known, for example the Rhenish Mountains and Harz Mountains of Germany (Nicolaus 1963; Korn 1990), the Antler Foreland Basin (Korn and Titus 2011) and the South Urals (Ruzhencev in Bogoslovsky *et al*. 1962; Ruzhencev and Bogoslovskaya 1971). It is thus not a phenomenon restricted to a distinct region but probably distributed worldwide. In so far as we can determine, these coarse wrinkle layer deposits with fingerprint-like patterns are known from spirally ornamented ammonoids of five regions.

Rhenish Mountains of Germany. The dorsal wrinkle layer similar to the pattern described here is known from two species of this region, *Goniatites globostriatus* (Schmidt, 1925) and *G. spirifer* Roemer, 1850 (Fig. 5A), both being ornamented with fine spiral lines that are slightly coarser than the growth lines (Korn 1990). The other three known species of *Goniatites* from the Rhenish Mountains, *G. hudsoni* Bisat, 1934, *G. crenistria* Phillips, 1836, and *G. fimbriatus* (Foord and Crick 1897), all lack spiral lines and possess a shell surface exclusively ornamented with crenulated growth lines and are known from very well-preserved material that does not show the wrinkle layer.

It is remarkable that other stratigraphically younger representatives of the family Goniatitidae that are spirally ornamented, such as *Arnsbergites*, *Paraglyphioceras* and *Lusitanoceras*, do not possess the wrinkle layer as described here. Furthermore, some spirally ornamented members of the family Maxigoniatitidae do not possess this structure; it is at least not recorded from *Beyrichoceras araneum* Nicolaus, 1963 and *B. mempeli* (Schmidt, 1941).

Anti-Atlas of Morocco. The genus *Goniatites* is represented by six species in the Anti-Atlas, of which four display spiral ornament. The wrinkle layer similar to the one described here is known at least from the two species *G. gerberi* Korn & Ebbighausen, 2006 and *G. tympanus* Korn *et al*., 2007 (Fig. 5B). The available material from the other two species, *G. stenumbilicatus* Kullmann, 1961 and *G. evelinae* Korn & Ebbighausen, 2006, is not adequate to determine whether a wrinkle layer is present or not. It is clear, however, that the species, *G. lazarus* Korn *et al*. 2005 and *G. rodioni* Korn & Ebbighausen, 2006,

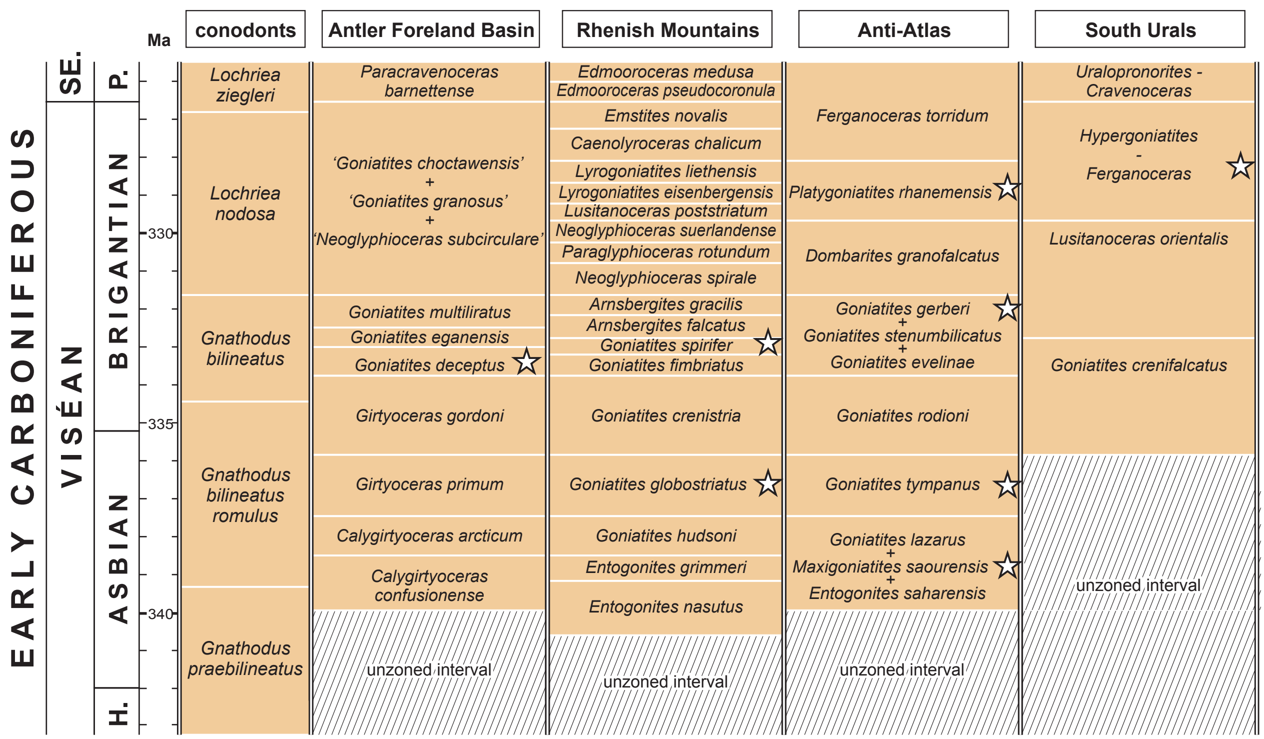

FIG. 6. Correlation between the Viséan ammonoid successions within various regions; the occurrences of ammonoids with the coarse wrinkle layer are indicated by asterisks (stratigraphical data from Ruzhencev and Bogoslovskaya 1971; Meischner and Nemyrovska 1999; Korn, *et al.* 2007; Korn and Kaufmann 2009; Korn and Titus 2011).

which lack spiral ornament also lack the wrinkle layer, as both are represented by well-preserved material.

Among the species co-occurring with *M. saourensis* in the same horizon, only *M. tafilaltensis* Korn *et al.*, 1999 displays the coarse wrinkle layer. The wrinkle layer has not been recorded from other species of the family Maxigoniatitidae, such as *B. elabiodiense* Korn *et al.*, 1999.

A prominent wrinkle layer has been recorded from stratigraphically younger assemblages. The spirally ornamented *Platygoniatites rhanemensis* Korn & Ebbighausen, 2006 displays such a structure (Fig. 5C), which, in its development and strength, is closely similar to the one seen in *M. saourensis*. The same pattern, but somewhat weaker, is also present in *Neogoniatites worki* Korn & Ebbighausen, 2006. By contrast, the spirally ornamented species of *Dombarites*, *D. granofalcatus* (Kullmann, 1961) and *D. bellornatus* Korn & Ebbighausen, 2006 do not possess the wrinkle layer.

Northern England. Some of the Viséan goniatites from the north of England show a coarse wrinkle layer similar to the species in the Rhenish Mountains. A spectacular example for the coarse wrinkle layer can be seen in *B. vesiculifer* (de Koninck, 1880) in the collections of the British Museum (Natural History), in which the structure is clearly visible at a rather small diameter (25 mm) in possibly mature specimens. However, *Goniatites moorei* Weyer, 1972 from Derbyshire is a species that closely resembles *G. globostriatus* but possibly lacks the dorsal wrinkle layer (Korn and Tilsley 2006).

South Urals. Ruzhencev (1960 and in Bogoslovsky *et al.* 1962) as well as Doguzhaeva (1981) figured a specimen of *P. molaris* (Ruzhencev, 1956) displaying the conspicuous wrinkle layer that resembles the patterns described here.

Antler Foreland Basin. Four species of *Goniatites* are known from the Chainman Formation of Utah and Nevada (Korn and Titus 2011), *G. americanus* Gordon, 1971, *G. eganensis* Korn & Titus, 2011, and *G. sowerbyi* Korn & Titus, 2011, all with an ornament consisting only of crenulated growth lines, and *G. deceptus* Korn & Titus, 2011 with delicate spiral ornament. Only the latter shows the coarse wrinkle layer in the dorsal body chamber, but its development is not as strong as in *M. saourensis* from the Anti-Atlas.

American Midcontinent. Goniatites multiliratus Gordon, 1962 fulfils the criteria of species that potentially could possess the wrinkle layer; however, the latter has not yet been reported. The well-preserved material from various localities suggests that this species does not show this structure.

COMPARISON OF THE TYPICAL WRINKLE LAYER WITH THE COARSE WRINKLE LAYER

The typical wrinkle layer, as originally described by Keyserling (1846) and Sandberger (1851), is characterized by delicate radial lines with a finger-print- or sand-dune-like pattern extending from the umbilical seam over flanks and venter of the dorsal whorl zone within the body chamber (see reviews by Walliser 1970; House 1971). In some cases, it continues from the dorsal whorl zone onto the ventral whorl zone accompanied by shortening of the elements and forming a structure called *Ritzstreifen* (Korn 1985; Sandberger 1851). Such a wrinkle layer has been reported from a number of different ammonoids throughout the history of the clade.

There are numerous Devonian ammonoids with distinct wrinkle layers such as the Givetian genus *Maenioceras*. *Ritzstreifen* are commonly visible in the Emsian genus *Gyroceratites* (e.g. Walliser 1970) as well as in some beloceratids from the Frasnian (House 1971). As far as the stratigraphic distribution is concerned, *Ritzstreifen* and wrinkle layers occur from the ammonoid ancestors via Emsian forms to the Famennian (particularly in the clymeniids; Doguzhaeva 1981; Korn 1985). Neither the Devonian wrinkle layers nor the *Ritzstreifen* ever become as strong as in the Viséan ammonoids described herein.

The coarse wrinkle layer differs from the 'normal' wrinkle layer in four aspects:

1. It is a structure with conspicuous three-dimensional morphology (in contrast to the flat 'normal' wrinkle layer) with the lamellae ranging for some distance (up to 3 mm) into the lumen of the body chamber.
2. The elements are very coarse, being arranged in distances of more than 1 mm, while in the normal wrinkle layer they are usually rather delicate and more closely spaced.
3. The coarse wrinkle layer in *M. saourensis* has a limited distribution within parts of the dorsal zone of the ammonoid. It covers a crescent-shaped area and wedges out towards the umbilicus and the ventrolateral shoulder.
4. The coarse wrinkle layer is probably restricted to adult specimens and does not occur earlier in the ontogeny, as in the normal wrinkle layer seen in subadult individuals.

DISCUSSION

We are not aware of any wrinkle layer development that approaches the one seen on the Early Carboniferous specimens from Morocco described herein with respect to strength. Much weaker wrinkle layers can be seen elsewhere, for example Middle Devonian *Maenioceras* and *Pharciceras*, as well as the Late Devonian *Probeloceras*, *Beloceras*, *Tornoceras*, *Pseudoclymenia*, *Cheiloceras*, *Sporadoceras*, *Platyclymenia* and *Wocklumeria* (Walliser 1970; House 1971; Doguzhaeva 1981; Korn 1985).

Several hypotheses to explain this extraordinary development of the wrinkle layer on these Moroccan specimens with respect to function have to be considered and may lead to different interpretations:

1. The coarse wrinkle layer is a product of a pathological condition, comparable with the Housean pits (de Baets *et al.* 2011). This explanation appears unlikely because this pattern occurs too regularly within the same species, but is completely absent in other species. Nevertheless, it could be a species-specific parasite, but this is also unlikely because the structure under consideration is confined to adults and absent in juveniles. A variation in the ontogenetic stage at which the infection happened would be likely, and thus, we reject this hypothesis.
2. The extra weight of the wrinkle layer was required to alter the buoyancy of the animal from a positively buoyant condition to a neutrally buoyant condition. We cannot determine whether this is a realistic scenario for the development of these coarse deposits, so this hypothesis must remain a possible explanation for now. However, the fact that many, if not all, specimens of certain species show this structure indicates that it represented no handicap for these animals.
3. These deposits were required to produce secure anchorage of the mantle and indirectly the soft parts within the body chamber. The probability for this explanation for the function of these deposits being correct is low because other ammonoids from the Devonian to the end of the Cretaceous only rarely have a moderate development of the wrinkle layer to enhance adhesion or attachment for the mantle tissue within the body chamber, and none to our knowledge have this coarse deposition of dorsal shell. By contrast, the attachment of the main muscles, namely the cephalic retractors, is very weak in all ammonoids and also in all coiled nautilids (Mutvei 1957; Mutvei *et al.* 1993). The reason for this is presumably that during growth, the muscles have to be detached and reattached frequently, which is well documented in fine growth lines within the attachment areas (e.g. Doguzhaeva and Mutvei 1991, 1996; Klug and Lehmkuhl 2004).
4. These three-dimensional deposits allowed greater advancement for the extension and retraction of the soft body within the body chamber. The major muscle scars that have been described (e.g. Doguzhaeva and Mutvei 1991, 1996; Richter 2001, 2002; Kröger, *et al.* 2005 for straight cephalopods) for this purpose

are located more or less laterally in the body chamber. There are also small and faint dorsal muscle scars in ammonoids, but no ammonoid muscle attachment scars have the shape and distribution of the wrinkle layer seen on the material described herein. Thus, it is unlikely that the main function of the coarse wrinkle layer deposits was to promote the movement of the body in and out of the body chamber.

5. An additional consideration is that the shape of the ridges of the coarse wrinkle layer deposits would enhance the forward movement of the body but the retraction of the body would be impeded and therefore very difficult. Nevertheless, the coarse wrinkle layer described herein increased the surface area contact of the mantle, and therefore, the overall adhesion of the soft body, but this might be simply be a 'spandrel' *sensu* Gould and Lewontin (1979) or 'fabricational noise' *sensu* Seilacher (1973) of a specific aspect of shell morphogenesis of these taxa with wrinkle layers (see number 7).
6. It has been suggested that the corrugated shape of septa might have increased the resistance of the shell towards hydrostatic pressure and predation attempts (see discussion in Hewitt and Westermann 1997). The same could be suggested for the coarse wrinkle layer. This hypothesis appears unlikely because there is no connection between the wrinkle layer and the lateral shell wall, and therefore, it has no effect on the mechanical strength of the outer shell wall.
7. The wrinkle layer in the dorsal whorl portion could be a 'fabricational noise' (Seilacher 1973) from shell growth. This hypothesis is supported by the fact that there are growth-related structures such as lirae or minor megastriae (Bucher *et al.* 1996 and references therein) in the outer shell that are similarly spaced as the wrinkles. Additionally, both the outer shell and the coarse wrinkles display fine growth lines. This implies that both structures grew simultaneously in the course of the periodic forward movement of the gradually increasing mass of the soft body in the body chamber during ontogeny. Possibly, this is also related to the deceleration of growth.

So why is there a coarse wrinkle layer only in the terminal body chamber? In many ammonoids and nautilids, dorsal shell and also the black layer become thicker when the animal approached adulthood and in the phase after maturity (Davis *et al.* 1996; Klug 2004; Klug *et al.* 2004). This is apparently the case in the material presented here. Small specimens of the same taxa lack the coarse wrinkle layer. Therefore, the onset of wrinkle layer growth might be linked with some kind of 'terminal countdown' (Seilacher and Gunji 1993). We suggest that these wrinkles represent some kind of internal collar-like megastriae (as in some Mesozoic lytoceratids; see Bucher 1997 or Hoffmann 2010), where shell secretion continues although longitudinal growth has stopped. Possibly, the rate of aragonite secretion was continuous, but because in these involute ammonoids, the distance covered dorsally is much smaller than ventrally, shell mass accumulated in a shorter distance.

Remarkably, the strongest wrinkles are not found at the umbilical wall but slightly more ventral (i.e. ventrolateral on the preceding whorl). This might have to do with the rapidly decreasing clearance towards the umbilical wall. If the wrinkles had kept their maximum width up to the umbilical wall, they would have almost completely closed this part of the body chamber. Potentially, this shell accumulation might have altered the location of the centres of mass and buoyancy, but this hypothesis cannot be tested with our material.

CONCLUSIONS

The function and phylogenetic distribution of the coarse wrinkle layer cannot be readily explained by a single hypothesis at this time. Nevertheless, our favoured explanation is that the coarse wrinkle layer represents a peculiar kind of growth-related form of an accumulation of dorsal shell comparable to collar-like megastriae on the outer shell. Dorsal shell formation begins in involute forms towards the termination of growth (Doguzhaeva 1981; Kulicki *et al.* 2001), which is also the case in the coarse wrinkle layer of the Carboniferous ammonoids under consideration. Possibly, this coarse dorsal shell accumulation can also be explained partially by the small umbilicus, that is, while the shell-secreting mantle covers a long ventral distance and secretes more aragonite, the distance in the dorsal part of the shell is much shorter but the mantle just cannot reduce shell secretion significantly. A similar effect can be seen in many oxyconic forms, which have strengthened umbilical walls or even umbilical extensions (e.g. Nassichuk 1967; Bogoslovsky 1969; Tozer 1972; Klug and Korn 2002; Monnet *et al.* 2011). One or more secondary functions that could involve this coarse wrinkle layer are also conceivable, although such functions are not possible to test at this time.

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